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BULLETIN
OF THE
TORREY BOTANICAL CLUB

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The development and structure of the bulb in *Cooperia Drummondii*

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(WITH PLATES 14-16 AND NINE TEXT FIGURES)

A survey of the literature dealing with the Amaryllidaceae and closely related families reveals the lack of detailed study of bulbs, such as modern methods of microtechnique and the compound microscope make possible. The usual textbook drawings of bulbs are extremely hazy as regards the nature of the vegetative point and even of the neighboring and slightly older members. The present study is submitted with the hope of supplying a more complete knowledge of the development and structure of a typical bulb, together with diagrammatic representations of the same.

HISTORICAL

Herbert (13), in his discourse on the Amaryllidaceae, states that the genus *Cooperia* has "black shelly seeds." He received his bulbs of *Cooperia Drummondii* (12) from travelers and grew them in his greenhouse or outdoors—according to season—as he did his other plants for study. "One bulb in six months produced five successive scapes," is his experience. "As soon as the seed on one scape is ripe another seems ready to rise. . . . Its habit appears to be to flower successively from earliest spring till September with leaves principally in autumn or winter." Flowering in the greenhouse at Brown University was at its best during March and February. No successive flowering of any one plant occurred extensively. Indeed it was deemed good fortune if

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several out of a dozen bulbs containing immature flowers blossomed at all. Although no criticism is intended here on either hand, it seems fair to state that Herbert was not justified in assuming that he could determine in European greenhouses or gardens the habit of bulbs native to Texas. He found his *Cooperia Drummondii* with a "flower [which] expands always in the evening, usually not perfect after the first night." Nocturnal flowering is an anomaly, as Herbert himself states, and it seems probable that he was overzealous here in his observations, since the writer over a period of three years observed no new flowers of *Cooperia Drummondii* except in the morning and also observed no flowers opening except in the bright morning light. In fact the flowers in the greenhouse rarely shoot up as late as after eight o'clock in the morning. It is claimed that the name "rain lily" is applied to this amaryllid on its native ground, because it does shoot up into full bloom on a bright morning after a period or night of rain.

Irmisch (16-18) described in detail the structure and development of many bulbs among the Liliaceae and Amaryllidaceae, and a short article on bulbs contemporary with Irmisch's works was published by Koch (20) in 1849. In this last paper bulbs are classified as perennial, periodic and biennial. We find in years subsequent to 1850 no important work undertaken on the bulb excepting the biological studies of Rimbach (23-28) published around 1897.

A number of articles, important indirectly if not directly, may, however, be recorded here for the future reference of other students. In 1870 Hanstein (10) published an article on embryo development in both monocotyledonous and dicotyledonous plants. The species of plants discussed in this work are of no immediate interest, yet the article deserves study and consideration because its author is a clear-headed pioneer in showing the relation of physiology to morphology and anatomy. Baillon (1) comes closer to the subject at hand while describing what seem to have been bulbiform abnormalities in the development of the embryos of *Hymenocallis*, *Crinum*, etc. The anatomy or structure of the vascular traces and secondary roots, and the relation of leaves and shoot axis in certain monocotyledons, e.g. *Allium Cepa* and *Lilium Martagon*, are well comprehended by Falkenberg (7).

The work of Šolms-Laubach (30) is known and well established in reputation. Tschirch (32) describes some interesting observations in regard to the cotyledon of *Lupinus* during its development in the seedling.

Baranetsky's work (2) on the development of vegetative points in monocotyledons is exceedingly valuable, discussing as it does among other points the development of subepidermal cambium, foliar buds, ensheathing leaves, internodes and permanent tissues for nine specific monocotyledons. It enters into details of anatomy further than the present paper makes any pretense of doing. A paper on the germination of the Amaryllideae by Worsley (36), delivered before the Royal Horticultural Society, is inaccurate and needs no consideration. The structure of a garlic bulb has been described in a general fashion by Highfield (14). The duration of bulb parts, the maturity of seedling plants, and the placing of the bulb slightly below the surface of the ground by means of roots formed from the base of the cotyledon are noted briefly. Howard (15) has experimented with the mature plants of *Cooperia Drummondii*, while working on the summer rest period of plants. He does not mention any studies with "offsets."

METHODS AND MATERIAL

The mature bulbs for this study of *Cooperia Drummondii* were secured from the campus of the University of Texas through the courtesy of Dr. H. H. York, of Brown University. A portion of the bulbs planted in the greenhouse at Brown University flowered freely and produced seed, which on maturity was used to secure all young plants.

The methods of microtechnique usually followed were found unsatisfactory, since the bulbs of *Cooperia Drummondii* appear to be particularly troublesome material for embedding. Their delicate scales contain starch, a mucilaginous slime which may coagulate during killing and fixation, and crystals of calcium oxalate (see Menz, 22). The scales and stem-axis are composed of parenchyma cells and vascular bundles, which resist the sectioning individually. Material was fixed in an aqueous solution of picro-acetic* acid allowed to act for twenty-four hours. A water

* 1 gram of picric acid, 1 c.c. of acetic acid, and 100 c.c. of water.

solution of the fixing agent was found preferable to an alcoholic solution, since in fixing material such as *Amaryllis* the alcohol evidently causes a coagulation of substances present in the scales and possibly in the bulb axis. To hasten the penetration of the material by the fixing agent, the object as soon as dropped into the acid was placed in a chamber from which the air was exhausted until the large size of the bubbles arising from the cut surface of the tissue indicated a fair approach to a vacuum. The air was allowed to replace the partial vacuum very slowly without outside aid. The use of the exhaust chamber was also resorted to with every change of alcohol, alcohol and ether, and ether. The fixation was practically perfect owing to more immediate and entire penetration. It did not, however, secure even moderately good fixation of incipient roots which were wholly within the bulb axis. Prior to killing and fixation, the bulb was trimmed down to about six scales, if the purpose was merely the examination of the youngest portions. Thorough fixation was thus more easily secured and the vegetative point was not crushed by the heavier parts.

Washing was carried on in water for two days and completed in the low grades of alcohol, such as 20-70 per cent. The general celloidin method was followed from here on until the actual point for embedding was reached. At this point in the work, the object, after the removal of the superfluous celloidin, was hardened in 70 per cent alcohol and then in chloroform for two hours. It was transferred from the chloroform to 85 per cent alcohol. The usual paraffin method of imbedding was now followed (5). Material prepared in this way sectioned with unusual smoothness and ease.

The rotary microtome was used in all paraffin work except where bulbs or pieces of material were too large for the section block. Such large pieces of material were mounted on blocks of wood, trimmed out underneath until small enough to be placed in the jaws of the sliding microtome clamp. In handling individual paraffin sections as large as, or larger than, two inches square, a vessel of warm water was kept at hand. The sections placed carefully on the surface of the warm water uncurled readily, with no danger of cracking. It is necessary to see that the water is not

too warm at first. A few changes of the water to warmer or reheating of the water by placing the container in another vessel of warmer water will be found useful.

MATURE EMBRYO

The structure of the mature embryo as seen in relief exhibits a scarcely protruding pocket, which protects the leaf-primordium and the vegetative point by surrounding their outer surface as they lie against the base of the cotyledon. The sheath-like base of the cotyledon has no vascular system and is very simple in structure. The long spindle-shaped cotyledon is succulent and projects into the mass of endosperm, absorbing food for the developing embryo by means of a layer of thin-walled parenchymatous cells running parallel with the longitudinal axis of the embryo. The suspensor, which is composed of either one or two cells, still holds the embryo in position at maturity.

The number and size of the leaf-primordia, developed at the time the seed is ripe, are not at all constant but depend on the individual embryo. No cases have been noted, however, where the first leaf-primordium had not made its appearance at this period. The primary root is protected by a well-developed root cap even as early as the maturity of the seed.

Wordsell (35) has recently given to botany a comprehensive paper on the monocotyledonous embryo, where extensive discussions and a bibliography relating to the cotyledon may be found. His opinion is exactly that of Čelakovsky, namely, that the cotyledon is an equivalent of the capsule of the moss sporogonium, just as the hypocotyl is of the seta. Goebel (8) states in regard to the cotyledon of the seed plants: "I need only say here that the cotyledons, which so frequently differ in form from the foliage leaves, are merely arrested forms of these, the arrest being sometimes permanent, sometimes transient." Lyon also has contributed (21) to discussions of the true morphological position of the cotyledon. At best a discussion becomes one of terminology unless combined with detailed anatomical observations on serial sections of embryos at successive ages of development. The present writer is inclined to agree with Lyon, stating that as the cotyledon of *Cooperia Drummondii* does not appear to arise as an

exogenous lateral outgrowth upon the growing point of a stem as do the later foliar structures, therefore, said cotyledon, occurring in the mature seed plant at the base of the primary stem, is more closely related to the nursing foot of the bryophytes. The succulent cotyledon of the young plant of *Cooperia Drummondii* in anatomical structure and size is well adapted to serve as an absorption organ.

SPROUTING OF THE SEED

The ripe seed of *Cooperia Drummondii* was described by Herbert (13) as having a brittle, shiny black seed coat and inclined to be wedge-like in shape. The seed coats are slightly torn at the time of sprouting as the root pushes through the very small micropyle, but they are never split apart into halves. On February 20, 1914, the seeds from a ripe pod were immediately placed upon wet filter paper on the sides of a moist chamber at ordinary room temperature. Three days later—February 23—the seeds had sprouted and the roots on the seedlings averaged 4 mm. in length; on February 25 the root length was 10–12 mm., while at thirty days of age the root length was 65 mm. If, however, the seeds were well dried and allowed to remain dry for several months at the temperature of the laboratory they did not sprout so readily.

The future root and shoot of the embryo are pushed out of the seed coats by a lengthening of the cotyledon, as well as by the growth of the root- and shoot-regions. Solms-Laubach (30) notes a similar condition in *Heteractia*.

The portion of the cotyledon between the micropyle region of the seed coats and the surface of the soil becomes a brilliant green, indicating the formation and presence of chlorophyll here. The cotyledon therefore functions in part as a leaf, aiding the leaf blades in the photosynthetic processes of the plant's activities. The leaf grows upward to the light above the ground, while the cotyledonary sheath serves as a protecting sheath in the same fashion as the encircling leaf base of any subsequent leaf serves as a sheath for the next younger leaf (FIG. 4). The region bounded by the root, the cotyledon and the plumule was designated by Richard (29) in 1808 as the "tigelle," corresponding as he said to the Latin term "cauliculus." The "tigelle" he defines as

merely a "prolongement" of the "radicule," explaining that "la Tigelle (Cauliculus) se confond d'une part avec la Radicule dont elle n'est qu'un prolongement et se termine de l'autre à la base de la cavité cotylédonaire." Jussieu (19) agrees with Richard and also connects the "tigelle" up with the term "carnode" of Cassini and with Brongniart's "mealy body" found in *Lemna*, although the describer says the latter even may be a cotyledon. At this region designated as the "tigelle" the writer noticed in *Cooperia Drummondii* that the cells divide in planes at variance with the tissues of the shoot above it and the root below it (FIG. 10, *h*). Here they divide in both the horizontal and tangential planes with little lengthening and practically no broadening, while in the shoot and root the cells broaden relatively rapidly and also elongate greatly.

The area enclosing the axis of the first leaves and the growing point (the plumule, the "gemmule" of early writers) is potentially cotyledonary. Lyon (21) states that the maximum development in this area takes place at the point or points that are in the most favorable position to function, and that in monocotyledons the maximum development occurs only on one side. And, further, that cotyledons *do not* arise as exogenous lateral outgrowths upon the growing point of a stem as do all later foliar structures. The gross anatomy of *Cooperia Drummondii* indicates that there is a point of maximum development and also one of decidedly minimum development in the cotyledonary region. Also the anatomy of the developing embryo shows us that the cotyledon does not develop from the vegetative point, nor does the cotyledonary sheath. The function of each of these portions is peculiar to itself, the maximum point of development elongating into a haustorial organ with the function of absorbing food for the germinating embryo, the point of minimum development not elongating but serving as a protective covering or a sheath to the primordia or a pocket in which the gemmule is deposited, according to the older writers, as a ball is in a cup. The gemmule is thus defined by Richard (29): "La Gemmule (Gemmula) est la petit corps simple ou composé qui naît ou du fond de la cavité cotylédonaire, qui le referme étroitement." The early scientists noticed that their "gemmule"—the vegetative point plus an

incipient leaf or so—could be sighted through the “fente.” As Jussieu (19) states: “. . . et ce ne fut qu’après des recherches répétées et minutieuses que je parvins à m’assurer que le cotyledon présentait en effect une petite fente vers sa base.” They speculated as to whether or not this gemmule were naturally detachable from the rest of the structure. Brown (3) speculates in his work and merely shoulders enough responsibility to say that the gemmule in bulbiform amaryllids can be seen and that it escapes through this opening, “petite fente.”

A careful microscopic examination of slides of a five-day-old *Cooperia Drummondii* seedling reveals cell structure indicating that root contraction has already begun. Such a condition has been noted by Hällström-Helsinke (9) in *Urginea maritima*, by Rimbach (23–28) and by De Vries (34) among the dicotyledons and also in *Hyacinthus orientalis*. Rimbach appears to be the best-known investigator volunteering a hypothesis of the relation of this contraction to root tissues. It is the intention of the writer to discuss his deductions and those of others later.

THE SEEDLING

A five-day-old plant of *Cooperia Drummondii* (FIG. 1) shows no outward indication of bulb formation. However, the region *h* does limit the territory of the root and of the shoot. The primary root is a tap root, in appearance stout, tapering slightly downward, and colorless. The shoot consists of the first leaf blade or lamina, *l*₁; the cotyledon, *c* (from which in the preparation drawn portions of the seed coats and of the endosperm tissue, *e*, had been removed); and the cotyledonary sheath. A central longitudinal section of this individual (FIG. 2), under the low power of the microscope, shows in addition the sheath, *b*₁, of the first leaf and the primordia of the second leaf, *l*₂ and *b*₂, together with the vegetative point, *pm*. The stippled strips represent approximately the space occupied by the vascular traces, no branch of which goes to the cotyledonary sheath, *cs*. FIG. 3 takes to one side the youngest area and represents exactly its cellular structure. In this region, surrounded by the first leaf of the young plant, the cells are actively dividing. The cells at *l*₂ and *b*₂ indicate not only that the second leaf has already become differentiated from the primordial meristem, *pm*,

but also that as a whole the meristematic tissue of this second leaf occupies an area placed diagonally to the longitudinal axis and surrounding the primordial meristem like a collar. The primordial meristem is often definitely composed of paired cells (FIGS. 3 and 6, *pm*), as Carano (4) has recorded for *Yucca*. Each new leaf arises from a group of subepidermal cells (Barenetskey, 2), which become meristematic and divide tangentially. Thus a new tissue is formed which, as it pushes out, becomes a future leaf. As the first leaf is thrust out far from the cotyledonary sheath into the air (FIG. 4), the cotyledon elongates and curves downward until it is parallel with itself and the vertical shoot, thus passing through an angle of 180 degrees (FIG. 4).

THE TWO-MONTH-OLD PLANT

When the food supply has been exhausted or drawn upon to the necessary extent the cotyledon, having no further need to serve as a haustorial organ, becomes shriveled up and dies (FIGS. 5, and 14). With this dying off of the cotyledon the dry, hard seed coats with any residue of endosperm drop to the ground or at least cease active relations with the cotyledon.

The second leaf blade usually reaches daylight between the fifty-fourth and the sixty-first day (FIG. 14). As the first leaf sheath is surrounded by the basal sheath of the cotyledon, so this second leaf sheath is surrounded by the basal sheath of the first leaf, in respect to which it is distichously placed. In *Tulipa* the leaf lamina, as is well known, does not always develop. Henry (11) makes note of this fact in his discourse, "Beiträge zur Kenntniss der Laubknospen." Even in young bulbs of *Tulipa* the aborted scale-like leaf alternates with a true leaf bearing a green lamina. In *Cooperia Drummondii*, however, the lamina always develops and as a result we have in this member of the *Amaryllis* family no mere sheath- or scale-leaves. The lamina of the leaf of *Cooperia Drummondii* appears to develop simultaneously with its respective base. The incipient bulb is now readily recognizable (FIGS. 5 and 14). Its outer and only scale is formed

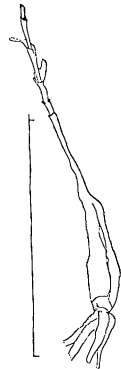


FIG. 1.
One-year-old
bulb; scale =
5 cm.

of the cotyledonary sheath. The bulge shown (FIG. 14) is due to a young root. This first adventitious root, *r*, originates (FIG. 8) at the node of the second foliar leaf and, growing downward, cuts its way through the first leaf and the cotylar sheath. A slightly older root with a well differentiated root cap and primary tissues (dermatogen, periblem, and pleurome) is shown in FIG. 18. This seedling is from the same planting as that of FIG. 8. The young root arising endogenously in the bulb- or stem-axis will, together with similar companions, replace the tap or primary root. The primary root is still active at this time. The secondary roots, which become functionally the principal roots of *Cooperia Drummondii*, are adventitious roots, derived from an active cambium tissue below and to one side of the growing point. They force their way through the tissue of the bulb-axis and form at first roots to one side of the early dying primary root and later a complete ring of such roots. The roots of *Cooperia Drummondii* have root hairs. The vascular bundles which develop in the secondary roots anastomose with the bundles already formed in the stem-axis. The complete working out of the origin and arrangement of the vascular traces in the stem-axis of *Cooperia Drummondii* would be very difficult, so complicated is the anastomosis. Both the primary root and the secondary roots show a wrinkling on their surface which is connected with the drawing down of the bulb into the soil by contraction of said roots. A bulb may be drawn down in this fashion to a depth of over seven inches.

The puckered or wrinkled condition of the primary roots (FIGS. 8, 15, 17 and 18) is due to contraction of at least some of the tissues. This phenomenon occurs in the adventitious roots also. Its hypothetical mechanics will be discussed later. The outlay of root tissue in FIG. 17 has a narrow slice marked off. This slice has been divided into three sections—1, 2 and 3. If this narrow strip of root is studied with the high power of the microscope we have under observation cellular tissues similar to those of FIG. 19, where 1 represents the vascular region; 2, the parenchyma; and 3, the cork and other dead tissues. Evidently the root contraction has entirely damaged only the outer cells, which are now dead tissue. The inner cells have in some way accommodated themselves in part to the strain. The trace is still intact although

its individual cells are irregular in diameter, presumably from the effects of some pressure. The parenchyma cells outside the trace are still equipped with cytoplasm and nuclei, although some force has pushed them by each other and flattened their nuclei.

ROOT CONTRACTION

The first reference in the literature to root contraction, according to De Vries (34), is that of Tittmann (31) in *Flora* for 1819. Under "Wurzelbildung" Tittmann describes the contraction of the roots in *Daucus Carota* as follows: "Der Stengel wird dicker und kürzer, zieht sich gleichsam in die Erde hinein, oder wird von derselben angezogen, und man findet dann nach einiger Zeit die langen Saamenblätter dicht auf der Erde ausgebreitet. Untersucht man in dieser Periode die Wurzel, so hat sich die Gränze zwischen ihr und dem Stengel, der sich nun auch in der Erde befindet, ganz verloren und ausgeglichen."

De Vries (34) himself worked principally with dicotyledons, experimenting with eighteen species of plants. He studied the effects of exposure to air, to water and to salt solutions on strips, separate pieces of definite tissues, and single cells of roots. He measured changes in length, width, and volume of tissues and cells. He considered roots from plants still bearing succulent cotyledons to those two years of age. He studied young roots and roots two years old. Each experiment is considered in itself and in the light of previous experiments, until at last he concludes that root contraction is not due to intake of water but to changes in turgor and remarks that the thoughtful reader will ask, "durch welche Ursachen die ungleiche Dehnbarkeit der Zellhäute selbst bedingt wird."

Rimbach discusses root contraction as it occurs in *Colchicum autumnale* (26), *Arum maculatum* (28), and *Allium ursinum* (27). He found that, in the case of naturally deep-set bulbs of *Allium ursinum*, a depth of 10-15 cm. was attained after several years by the contraction of the roots. In explanation as to how contraction in roots comes about he states, that, while the root tip holds firmly to the earth particles, the endodermal cells contract longitudinally as a result of a tendency to lengthen radially and tangentially, which results in the contraction of the root. The bulb yields to

this pull, which results from the contraction of the roots, and is gradually placed more deeply in the ground with each new set of roots. Even the upward development of the shoot, where the lowest and oldest scales are each formed at a slightly higher level, does not counteract entirely this forced downward movement of the bulb. Therefore the bulb is continually placed more deeply in the soil.

In *Arum maculatum* Rimbach (28) explains that the active portion of the root consists of the cells directly below the epidermis and the "hypodermal layers." These cells shorten in their length as much as one half and their radial walls lengthen somewhat. The vascular bundles and their accompanying cells are not active. However, the latter respond sufficiently to the vertical pressure caused by the shortening of the parenchymatous cells just outside them to show definite wrinklins along their walls, and the tracheal tubes themselves shorten between the rings.

Rimbach's careful observations and well-chosen biological experiments are not supported by his theoretical conclusions. Because he has accurately noted that endodermal cells lengthen radially, he proceeds to state that they shorten longitudinally and that therefore the whole root contracts, with the result that the bulb is set more deeply into the ground. All other tissues are passive, yet they must be shortened in the shortening of the whole root. Without sufficient morphological proof Rimbach claims that the outer or cork cells are crushed and killed, and that the vascular cells are thickened. The outer cells are crushed doubtless, but do they die first or are they killed by the crushing? His further conclusion that the vascular cells thicken may be true, but where is his proof? To return to the active or endodermal cells, how can we accept the statement that because a cell lengthens in one direction therefore it must necessarily shorten in another? Volume being constant and cell wall composition and tension being similar at every point this would be true; but Rimbach did not investigate these points.

Rimbach states that ripples may be seen on the root surface even to the root-ends with the naked eye. Microscopic slides have proved to the writer that the process of root contraction is well under way in a five-day-old seedling of *Cooperia Drummondii*

at points not visible to the naked eye. The ripples in individual cells are not confined to radially placed cell walls, as Rimbach finds them to be in the species which he investigated. On the contrary they may be found on walls running in any direction. In some stages they are so fine as to be distinguishable only with the oil immersion objective, but always numerous cells with rippled walls may with care be detected in the parenchyma cells of the root with a combination of 10 ocular and 8 objective.

The warped and altogether disorganized condition of the epidermis and "hypodermal" layers in the contracted roots of *Cooperia Drummondii* may be comprehended, if we study the tissues represented by the blackened areas in FIG. 17, section 1.

It seems safe to accept these facts: (1) roots do shorten; (2) the parenchymatous tissues of the root are the seat of this activity; (3) the cork and the vascular trace are passive; (4) the cork is ultimately crushed; (5) there is a region where one can see wrinklins and measure shortening, a second region where no wrinklins are visible yet where one can measure shortening, and an unchanged region (Rimbach); (6) in dicotyledons the trace becomes visibly curved inward and outward in a wavy fashion, while in monocotyledons the vascular bundles remain practically straight (De Vries).

What remains to be determined constitutes a problem of botanical research as yet unsolved. We may hope that some worker with an interest in morphology as well as physiology may master this problem by a study of serial sections of young roots and a consideration of the physical relation of turgor and biochemical alterations in the protoplast and cell membrane.

All the roots of a plant may not shorten equally. *Phaedranassa chloracea*, according to Rimbach (25), has a main root which shows no shortening. In other cases none of the roots shorten. *Tulipa*, according to Döring (6), is a case in point. The bulb here would not be pulled down since its roots spread out almost parallel with the surface of the soil.

THE SCALES

The scales, that is, the leaf sheaths, which constitute the greater portion of the bulb, are differentiated into certain tissues, represented diagrammatically in FIG. 7. A scale has an epidermal

layer on each surface. The several rows of cells directly below the outer epidermis contain starch, while the cells below the inner epidermis do not. The starch-filled cells measure $59\text{--}158\ \mu$ in length and $59\text{--}69\ \mu$ in width, with their greatest dimension running parallel to the longitudinal axis of the bulb. The vast majority of such cells average $158 \times 59\ \mu$. The cells between the cells containing starch and the accompanying cells contain raphides in the first seven or so scales, but rarely in the older scales. The amount of starch also is less in the older scales than in the more actively functioning portions of the bulb. There appear to be, however, sphaero-crystals stored in the older scales. There is noticeably less starch and fewer raphides in the scales immediately

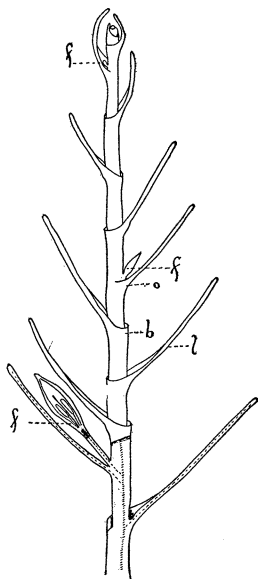


FIG. 2.

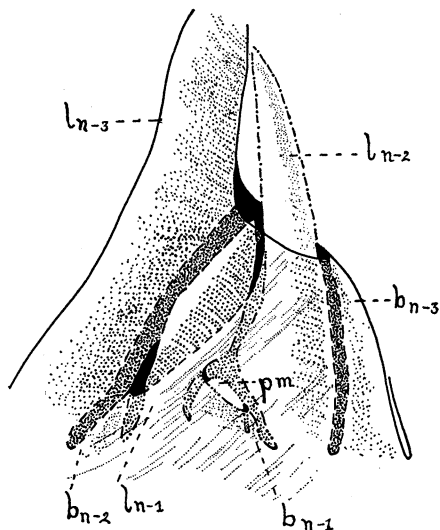


FIG. 3.

FIG. 2. Diagram of *Cooperia Drummondii* as it would appear if the internodes developed: *l*, lamina of a leaf; *b*, basal sheath; *o*, leaf subtending flower; *f*, flower; in the lower part of the figure a central longitudinal section is represented, showing principally the relation of the basal sheath to the main axis; the relation of the flower and its subtending leaf to the main axis is problematic with the evidence at hand.

FIG. 3. Diagrammatic semi-transparency of the youngest portion of the bulb of *Cooperia Drummondii*: *pm*, the primordial area, below which are the primordia of the youngest or *n*th leaf; successively older leaves are marked *l*_{*n*-1}, *l*_{*n*-2}, and *l*_{*n*-3}; their respective bases, *b*_{*n*-1}, *b*_{*n*-2} and *b*_{*n*-3}.

following the flower stalk which has most recently died, and finally neither starch nor raphides are to be noticed in the outermost and oldest scales. The leaf bases in the youngest portion of the bulb—the only portion within the bulb itself where the leaf base in cross section is scarcely continuous with the lamina—have no starch stored in them. The leaf accompanying the flower is supplied with starch even when it is very young. Young roots that have not yet pierced the bulb-axis contain raphides. The starch grains and raphides, therefore, are most prevalent in the younger scales. Here cells with raphides may be found among the tissues containing starch or scattered between the starch-bearing cells and the accompanying cells, but most commonly they are found in rows of cells. An individual cell in such a row is about twice as long as a starch-bearing cell or often still longer. The sheath or bundle of crystals practically fills the cell containing it. Measurements of the raphide-bearing cells show that their dimensions measure $277-475\ \mu$ in length and $79-99\ \mu$ in breadth. The remainder of a scale is composed of vascular bundles and their accompanying parenchyma, the cells of which are intermediate in length between the cells filled with starch and those with raphides. The dimensions of these rather simple cells range from $178 \times 119\ \mu$ to $297 \times 69\ \mu$.

Miss Menz (21) has made observations similar to the above in connection with *Amaryllis*, *Zephyranthes*, *Sternbergia*, *Crinum* and *Allium*, finding in the scales of these genera starch, raphides of calcium oxalate and also a latex-like or slimy substance stored as reserve material.

DEFINITION OF A BULB

Bulbs, according to Irmisch (16), have been looked upon as roots, underground shoots, and downward growing shoots, while Irmisch himself concludes with the emphatic statement that a bulb is a bulb—an organ peculiar to certain plants and distinctive in itself.

A bulb is a shoot in which the internodes have not developed or have developed only to a small extent (TEXT FIGS. 1, 4 and 5). The peripheral layers of the bulb consist of the bases of the foliar sheaths. As there are no internodes in the shoot of *Cooperia Drummondii* its foliar sheaths never can form an exterior covering

to internodes but instead surround the next younger sheath, as they themselves are surrounded by an older sheath.

If a shoot, developed as is usual in herbaceous plants, corresponds to a telescope drawn out for observation of the stars, a bulb finds its correspondent in the same telescope pushed in—i.e. a bulb is a foreshortened or a “telescoped” shoot (TEXT FIG. 2). A bulb of *Cooperia Drummondii* is probably never raised above the earth’s surface. It is constantly being set deeper into the ground. The oldest tissue composing the base of the truncate bulb axis is continually sloughing off, while the youngest tissue is continually formed at a point farther and farther away from the point where the primary root originated. This setting of the bulb deeply into the ground is due to root contraction, which has been explained as far as is possible with our present knowledge before us. An old bulb of *Cooperia Drummondii* may ultimately bear a neck 15–18 cm. in length.

“OFFSETS”

The “offsets” or “splits” arise between the mature scales as protrusions. When conditions fostering vegetative propagation occur, the “splits” develop (FIGS. 12 and 13; TEXT FIGS. 4 and 5) between the scales or leaf sheaths and break their way through the

outer and older bulb scales, in an effort to reach the soil. They develop on alternate sides of the axis and frequently occur between every five scales. However, there seems to be considerable variation in regard to this matter of arrangement.

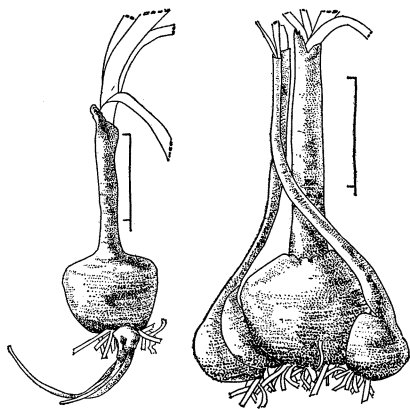


FIG. 4.

FIG. 5.

FIG. 4. “Offset” readjusting itself after an unfavorable start; roots diagrammatic, i. e. wrinklins due to contraction omitted; scale = 5 cm.

FIG. 5. Vegetative propagation displacing flowering; roots and leaves diagrammatic; scale = 5 cm.

Henry (11) notes that *Gagea arvensis*, *G. stenopetala* and

Tulipa sylvestris show secondary bulb formation from the original bulb developed to extreme abnormality, yet every bulb so formed is always a leafy shoot. That is, such a bulb is a secondary or lateral shoot, or a terminal shoot which will eventually separate itself from the growth of previous years. Vigier (33) relates a few casual but interesting experiments with bulbil formation in cuttings of *Lillium candidum*. Bulbils did not form on the cuttings, unless the end of the cutting and thus the terminal bud were injured accidentally or intentionally. Nipping the terminal bud of horticultural plants to produce lateral branching is a common horticultural practice. Regarded as lateral branches these bulbils are unique only in their being vegetative outgrowths which can of themselves reproduce the plant vegetatively, where the usual secondary branch can not do so without the gardener's aid. The bulbils of *L. candidum*, formed in the light above ground, were in Vigier's experiments green with purple spots, while those formed on the part of the cutting under the soil were white. There can be no proof brought up against the statement that there is primarily no difference between these bulbils of *L. candidum* formed below or above the ground and the offsets, splits, or brood-bulbs of *Cooperia Drummondii*, for instance. There is no difference even between the bulbils formed in Vigier's experiments: whether the said bulbils have green and purple pigment or are colorless; whether they are formed above or below the surface of the ground; or whether we are considering a bulbil or what is recognized commonly as a lateral shoot. In each case we have a shoot—a structure which is still a shoot none the less, whether it be a main or lateral shoot, or an artificially aborted shoot, or (as is the bulb) a naturally aborted shoot, in which the internodes have elongated little if at all.

THE MATURE BULB

Irmisch (16, 17) describes the structure of immature and mature bulbs of *Amaryllis formosissima* (now *Sprekelia formosissima*). His work presents to us a most careful research, recorded by the observer's skilfully executed drawings. While further investigation since 1850-60 causes us to feel certain in regard to points which are here discussed rather lengthily and

left undecided even then, and to disagree with some conclusions which Irmisch does draw, yet the ground is covered so minutely and the observations are presented so carefully that the work is worthy of our close consideration. According to Irmisch *Amaryllis formosissima* has in the mature bulb, considered first of all from the outside toward the inside, three or four leaves with

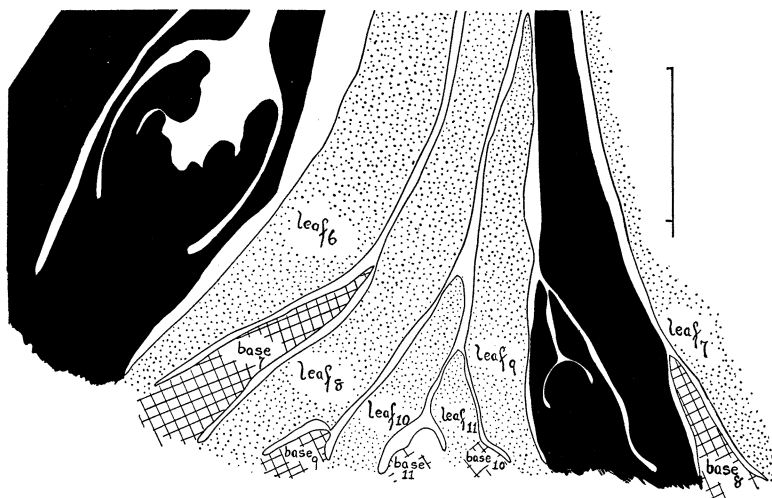


FIG. 6. Central longitudinal section of youngest portion of mature bulb; camera-lucida drawing of portion cut off between dotted lines at center of PLATE 16, FIG 17: black areas represent the flower and its subtending leaf; stippled areas indicate the portions of the leaves which becomes laminae; cross-hatched areas show the leaf bases; plain areas are primordial tissue; it is presumed that the oldest leaf shown is the sixth leaf—an arbitrary choice. Scale = 0.1 mm.

closed bases. Such a leaf he terms "Schale," which literally translated into English means "skin" or "hull" and again has the derived meaning, "bowl." This seems a most apt scientific term, for one can readily understand that if the center of a bulb is removed, leaving only a few outer scales there is left merely a few skins, bowl-like in shape. Following the three or four leaves with closed bases, there is one leaf with an open base which subtends a flower scape. Such a leaf is termed by Irmisch "Schuppe," which means "scale" (as of a fish) or "shovel" in English. Apart from the blade the open based leaf accompanying the flower of *Cooperia Drummondii* is shaped decidedly like a scale and with

the blade attached becomes the shovel. In the case of *Amaryllis formosissima* there is in the axis of this open based leaf an axillary shoot or secondary branch whose terminal bud becomes a flower. This flowering scape has two leaves which are not normally developed. The flowering branch is followed by three or four leaves with closed bases similar to the first group, but always growing smaller and more rudimentary as the primordia are approached. An old bulb might have within it four flowers with their accompanying "Schuppen" and thirteen to fifteen scales. Usually all laminae are dead at flowering times, Irmisch states, and the new leaves come always from that portion of the bulb inside of the last flower. The occasional open leaf does not alternate with the closed leaves, so that diagrammatically Irmisch's interpretation might be represented as in TEXT FIG. 7, *a*. In *Galanthus* and *Leucojum*, however, Irmisch does find alternation between Schuppe and Schale (TEXT FIG. 7, *b*). The present writer has observed for *Cooperia Drummondii* the same relation of the two types of leaves as Irmisch did for *Amaryllis formosissima*, which again relates *Cooperia* closely to *Amaryllis*. In *Cooperia Drummondii*, however, the axillary bud develops only one bract besides the flower from its terminal primordium. This is represented diagrammatically by TEXT FIGS. 2 and 9.

The shovel-like leaf accompanying the flower is open at the base in *Cooperia Drummondii* whether the flower matures or not, but in *Narcissus* and *Leucojum* the base of the same type of leaf becomes closed if the flower never develops. In *Cooperia Drummondii* this leaf may belong to the lateral axis which gives rise to the spathe-like bract and the flower. *Cooperia Drummondii* has no stipules unless the base opposite the lamina was once formed by the fusion of such (TEXT FIG. 8). It seems, however, as if the base were here derived from a slight and all-encircling outgrowth of the primordial meristem of each individual leaf primordium.

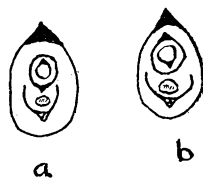


FIG. 7. Cross-section diagrams after Irmisch; *a*, of *Amaryllis formosissima*; *b*, of *Galanthus* or *Leucojum*; in *Galanthus* and *Leucojum* Irmisch found alternation between "Schuppe" and "Schale"; in *Cooperia Drummondii* and *Amaryllis formosissima* the open-based leaf subtending the flower does not alternate with the closed leaves.

The mature plant of *Cooperia Drummondii* has a subglobose bulb, increasing in size with age. The outermost scales have become thin, dry, brown membranes, whose venation is readily

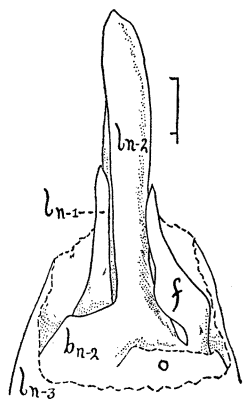


FIG. 8. Central portion of bulb showing immature flower; presuming there are n leaves, the first left we see is the $n-1$ leaf, which is surrounded by the $n-2$ leaf with its base and lamina designated as b_{n-2} and l_{n-2} respectively. This is in accordance with FIG. 3; f , an immature flower, and o , its subtending leaf with an open base. Scale = 0.15 mm.

seen. As one goes inward, tearing away the scales, those with dried edges are succeeded by fresher and thicker scales. Every third scale is separated from the next younger or older scale, according as we work inward or outward, by a scale accompanying a flower peduncle, and this arrangement is repeated in accord with the age of the plant, the parts always growing smaller and more rudimentary. An old bulb may contain the vascular traces and dried stalks of numerous past or undeveloped flowers, and immature flowers for three successive flowerings (see TEXT FIG. 9).

Irmisch (16) gives a type classification of bulbs supplemented with examples, Latin designations and a set of symbols. The first type is designated as "*Gagea*-Arten," and the symbol expression corresponding is $G+Z$, where G is equivalent to "*Gegenwart*" and Z equals "*Zukommen*," next year's development. Therefore all bulbs similar to *Gagea* consist of G (present, active portions) and Z (tissues capable of repeating the life story next year). Another type, e.g. *Galanthus nivalis*, is represented by the symbols $1V+G+Z$. $1V$ is equivalent to parts of the preceding year which are now present as "*Nahrblätter*" or sheaths containing stored material. Yet another type, *Amaryllis formosissima*, may be represented by $2V+G+Z$, where the parts of two previous years still remain. *Cooperia Drummondii* might be represented by $nV+G+Z$ where n varies largely with environment as well as with the age of the plant.

The following scheme, illustrating a mature bulb of *Cooperia Drummondii*, may likewise be considered in connection with TEXT FIGS. 2, 6, 8 and 9:

MAIN AXIS OF BULB

Three leaves with closed bases (Schalen).

Lateral axis:

One leaf with open base (Schuppe), position problematic;

One bract subtending flower;

One flower (terminating lateral axis).

Three leaves with closed bases.

Etc. to vegetative point.

Galanthus and *Leucojum* also have open-base leaves succeeded by a flower stalk, but their open-base leaves alternate with the closed-base leaves. The open leaves do not alternate with the

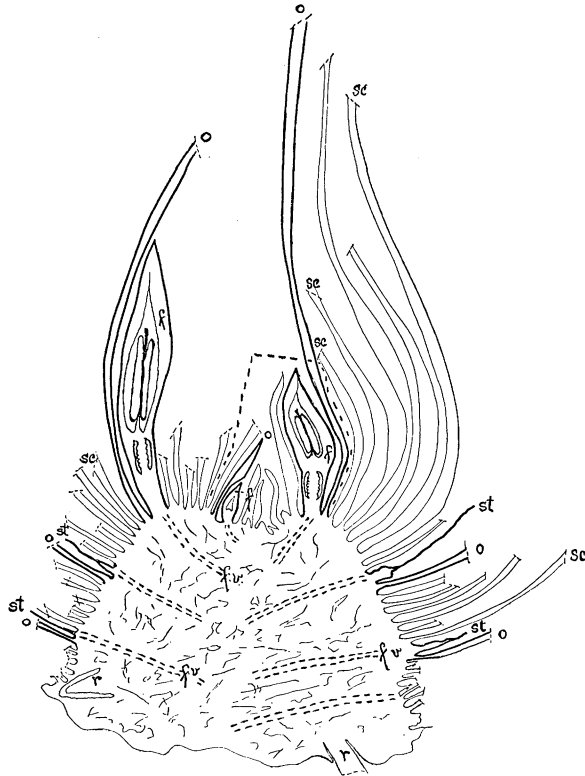


FIG. 9. Diagrammatic longitudinal section of mature bulb showing the main axis drawn in thin lines; the flowering axis (?) in heavier lines; the section between the dotted lines may be seen enlarged in TEXT FIG. 6.

closed-base leaves in either *Amaryllis formosissima* or *Cooperia Drummondii*, but with each other (TEXT FIG. 7, *a* and *b*). The

flower peduncle, terminal in respect to the lateral axis, is subtended by a spathe-like bract.

CONCLUSIONS

1. The mature seed of *Cooperia Drummondii* germinates with little difficulty.
2. A five-day-old seedling shows a tap root, hypocotyl, and one young leaf blade.
3. A ten-day-old seedling exteriorly shows no indication of bulb formation.
4. Seedlings by their fortieth to fiftieth day of growth have developed a typical bulb formed from the closed bases of alternate leaves.
5. The bulb is set deep into the ground by a contraction of the roots, which begins as early as the fifth day.
6. A mature bulb is composed of a thickened axis (with morphologically aborted internodes), from which develop (in a downward direction) adventitious roots, piercing the outer edge of the axis in a circle, and (in an upward direction) scales (leaf bases), flower scapes (each with its accompanying open base leaf), and leaves.
7. The flower scape and the leaf accompanying it alternate with the next younger corresponding leaf and scale; they arise between every third and fourth scale.
8. Vegetative buds of a type called "offsets" among horticulturists develop between the scales whenever conditions of environment are unfavorable to flowering.
9. A bulb is a foreshortened vegetative shoot which appears aborted, because the internodes do not develop, while the nodes are thickened by irregular and considerable multiplication of cells.

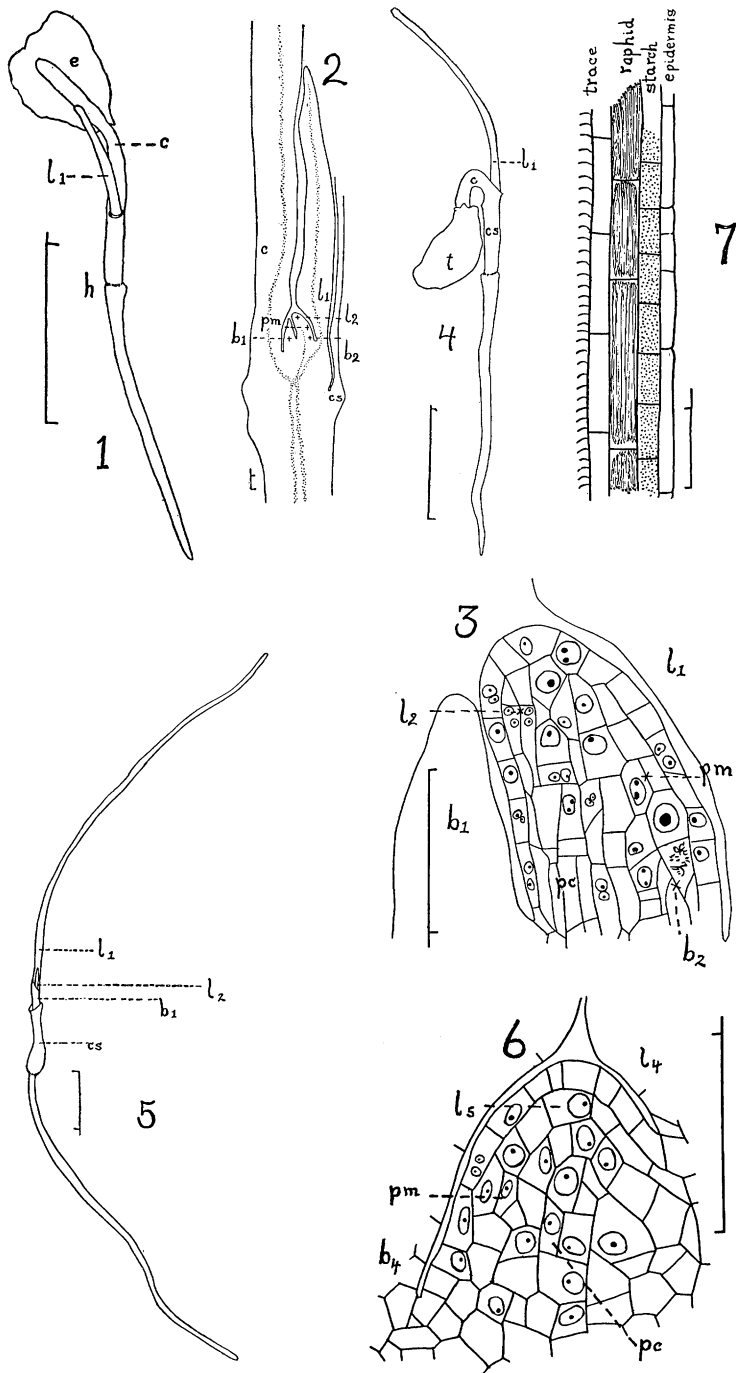
This paper was presented in 1918, in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Brown University. The writer begs to acknowledge the assistance given by Professor Harlan H. York of the Botanical Department.

LITERATURE CITED

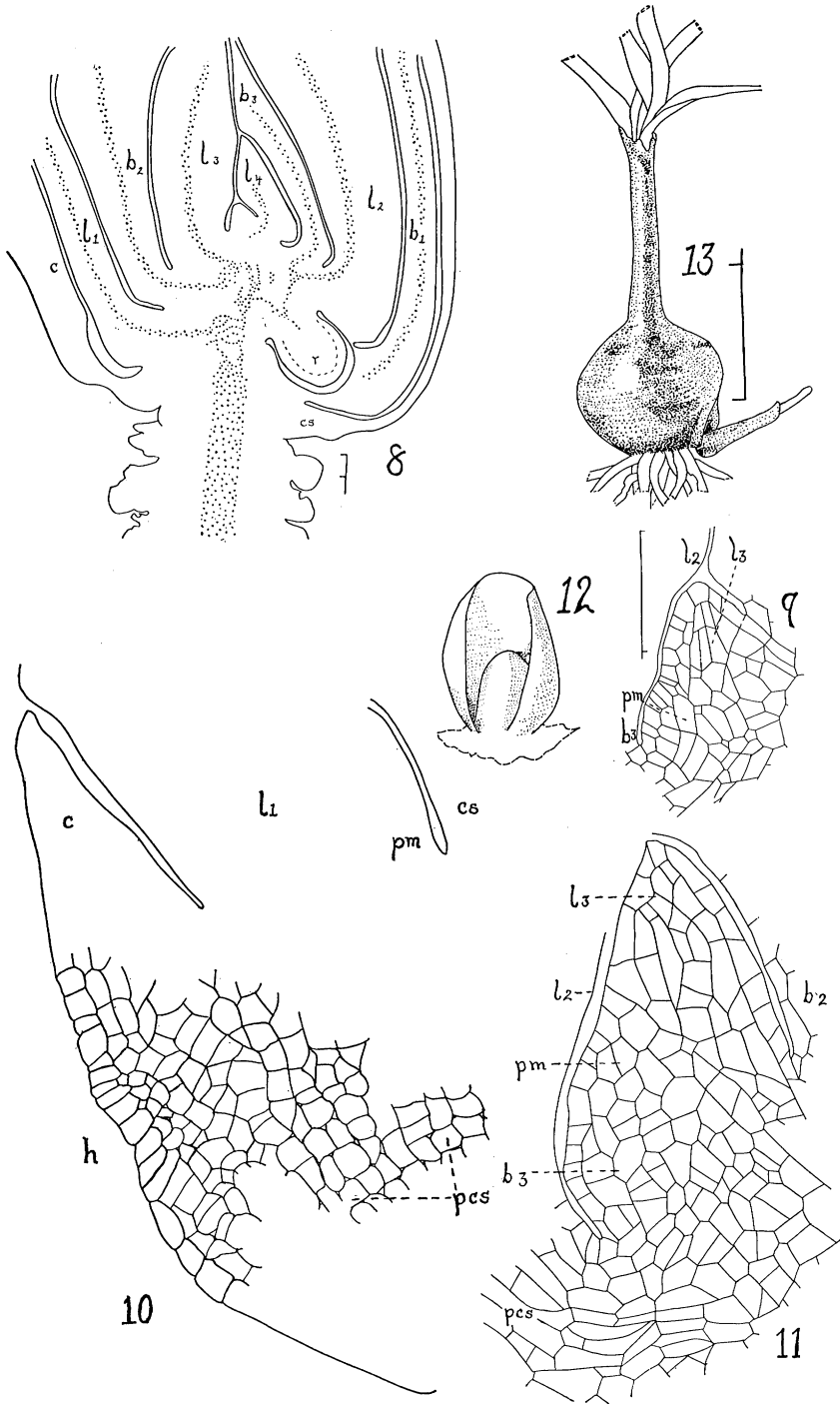
1. Baillon, M. H. Sur le développement et la germination des bulbi-formes des Amaryllidées. Bull. Soc. Linn. Paris 1: 4-5. 1874.

2. **Baranetzky, M. J.** Sur le développement des pointes végétatifs des tiges chez les Monocotylédones. Ann. Sci. Nat. Bot. VIII. 3: 311-365. pls. 14-16. 1897.
3. **Brown, R.** Prodromus Florae Novae Hollandiae et insulae Van Diemen. London. 1810.
4. **Carano, E.** Sulle formazioni secondarie nel caule delle Monocotiledoni. Ann. di Bot. 8: 1-42. pls. 1-4. 1910.
5. **Church, M. B.** Celloidin-paraffin methods. Science II. 47: 640. 1918.
6. **Doring, E.** Das Leben der Tulpe. Sondershausen. 1910.
7. **Falkenberg, P.** Vergleichende Untersuchungen über den Bau der Vegetationsorgane der Monocotyledonen. Stuttgart. 1876.
8. **Goebel, K.** Organography of plants. English translation. Oxford. 1900-05.
9. **Hällström-Helsinki, K. H.** Ueber die Keimung von *Urginea maritima* Baker. Schweiz. Wochenschr. für Chem. und Pharm. 49: 89-91. 6 figs. 1911.
10. **Hanstein, J.** Entwicklung des Keimes der Monokotyle und Dicotyle. Bot. Abhandl. 1: 1-112. pls. 1-18. 1870.
11. **Henry, A.** Beiträge zur Kenntniss der Laubknospen. Dritte Abtheilung. Nova Acta Acad. Caes. Leop. Carol. 21: 277-292. pls. 16, 17. 1844.
12. **Herbert, W.** An appendix (to the Botanical Register), containing a treatise on bulbous roots. London. 1821.
13. ——— Amaryllidaceae; preceded by an attempt to arrange the monocotyledonous orders, and followed by a treatise on cross-bred vegetables and supplement. London. 1837.
14. **Highfield, E. G.** The structure of a garlic bulb. Naturalist 1912: 331-336. 1912.
15. **Howard, W. L.** An experimental study of the rest period in plants. The summer rest of bulbs and herbaceous perennials. Second report. Missouri Agri. Exp. Sta. Research Bull. 15: 1-25. figs. 1-8. Ap 1915.
16. **Irmisch, T.** Zur Morphologie der monokotylichen Knollen- und Zwiebelgewächse. Berlin. 1850.
17. ——— Notes on the development of bulbs and tubers (abridged from the German original). Jour. Roy. Hort. Soc. London 8: 91-124, 207-221. 38 figs. 1853.
18. ——— Beiträge zur Morphologie der monokotylichen Gewächse. 1. Heft. Amaryllideen. Halle. 1860.
19. **Jussieu, A. de.** Mémoire sur les embryons monocotylédons. Ann. Sci. Nat. Bot. II. 11: 341-361. pl. 17. 1839.

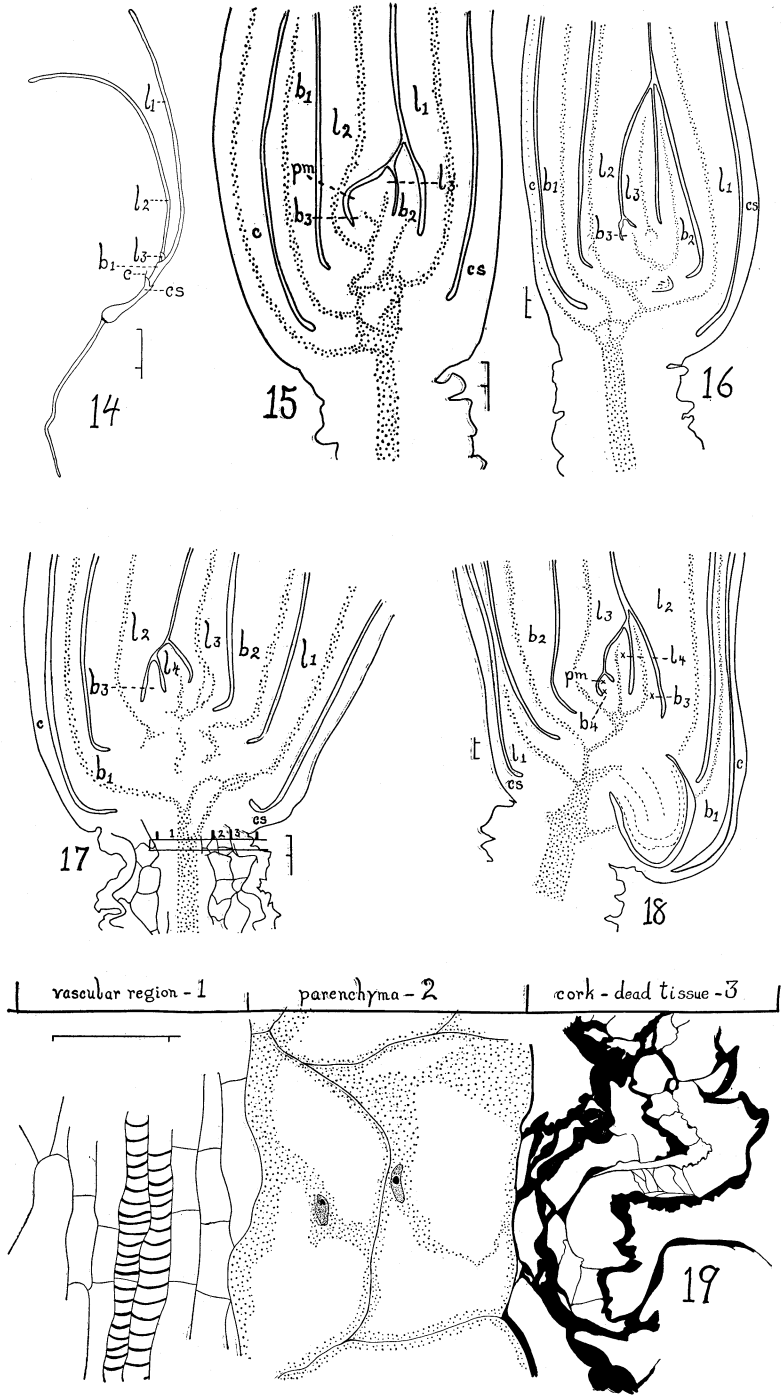
20. **Koch, K.** Lilienpflanzen und Zwiebelbildung [in Beiträge zu einer Flora des Orientes]. *Linnaea* **22**: 213-219. *pl.* 2. 1849.
21. **Lyon, H. L.** The phylogeny of the cotyledon. *Postelsia* **1901**: 57-86. 1901.
22. **Menz, J.** Beiträge zur vergleichenden Anatomie der Gattung *Allium* nebst einigen Bemerkungen über die anatomischen Beziehungen zwischen Allioideae und Amaryllidoideae. Sitzungsab. Kais. Akad. Wissensch. Wien **119**: 475-533. *pl.* 1-3 + *f.* 1-16. 1910.
23. **Rimbach, A.** Ueber die Ursache der Zellhautwellung in der Endodermis der Wurzeln. *Ber. Deuts. Bot. Ges.* **11**: 94-113. 1893.
24. ——— Zur Biologie der Pflanzen mit unterirdischen Spross. *Ibid.* **13**: 141-155. *pl.* 14. 1895.
25. ——— Ueber die Tieflage unterirdisch ausdauernder Pflanzen, *Ibid.* **14**: 164-168. 1896.
26. ——— Ueber die Lebensweise des *Arum maculatum*. *Ibid.* **15**: 178-182. *pl.* 5. 1897.
27. ——— Lebensverhältnisse des *Allium ursinum*. *Ibid.* **15**: 248-252. *pl.* 8. 1897.
28. ——— Biologische Beobachtungen an *Colchicum autumnale*. *Ibid.* **15**: 298-302. *pl.* 12. 1897.
29. **Richard, L. C.** Demonstrations botanique, ou Analyse du fruit considéré en général. Paris. 1808.
30. **Solms-Laubach, H.** Ueber monocotyle Embryonen mit scheitelbürtigem Vegetationspunkt. *Bot. Zeit.* **36**: 65-74, 81-93. *pl.* 4. 1878.
31. **Tittman, D. J. A.** Botanisch-karpologische Bemerkungen. *Flora* **2**: 651-666, 667-671. 1819.
32. **Tschirch, A.** Physiologische Studien über die Samen, insbesondere der Saugorgane derselben. *Ann. Jard. Bot. Buitenzorg* **9**: 143-183. *pl.* 20-25. 1891.
33. **Vigier, A.** Formation de bulbilles sur le lis blanc. *Rev. Hort.* **78**: 406. 1906.
34. **Vries, H. de** Ueber die Kontraction der Wurzeln. *Landw. Jahrb.* **9**: 37-80. 5 *figs.* 1880.
35. **Wordsell, W. C.** The morphology of the monocotyledenous embryo and of that of the grass in particular. *Ann. Bot.* **30**: 509-524. *f.* 1-10. 1916.
36. **Worsley, A.** Germination of Amaryllideae. *Jour. Roy. Hort. Soc.* **28**: 420-423. *f.* 110-112. 1903-1904.



CHURCH: COOPERIA DRUMMONDII



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Explanation of plates 14-16

The following remarks refer also to the text figures. FIGS. 7, 12 and 13 in the plates and TEXT FIGS. 1, 4, 5 and 9 are not camera lucida drawings. All other drawings except the diagrams are camera lucida drawings from actual living plants or microtome sections of the identical plants. Except for FIG. 10, where a Bausch and Lomb camera lucida was used, the Zeiss camera lucida was employed. A Leitz-Wetzler compound microscope was used as a rule. FIG. 10, however, was made with a Zeiss microscope. The longitudinal sections were cut in a plane at right angles to the broad surface of the lamina of the leaf. The scale of magnification is indicated for most of the figures. The following symbols are employed: *b*, leaf base; *c*, cotyledon; *cs*, cotyledonary sheath; *e*, endosperm; *f*, flower stalk; *fv*, flower trace; *h*, bulb-axis or "tigelle"; *l*, lamina; *o*, open-base leaf; *pc*, procambium; *pcs*, procambial strand; *pm*, primordium of stem; *r*, root; *sc*, closed leaf; *st*, old flower stalk; *t*, testa.

PLATE 14

FIG. 1. Five-day-old seedling; one half of the seed coats and the endosperm has been removed to show the cotyledon; *h* is the hypocotyl, and *l*, the first leaf; see FIGS. 2 and 11; scale = 1 cm.

FIG. 2. Central longitudinal section of five-day-old seedling, showing the sheath, *b*₁, of the first leaf, *l*₁, and the primordia of the second leaf, *l*₂ and *b*₂, together with the vegetative point, *pm*; the stippled areas show the location of vascular traces; scale = 0.1 mm.

FIG. 3. Vegetative point of five-day-old seedling (see FIGS. 1 and 2 for comparison); in this region surrounded by the first leaf of the young plant cells are actively dividing; the cells at *l*₂ and *b*₂ indicate not only that the second leaf has become differentiated from the primordial meristem, *pm*, but also that as a whole the meristematic tissue of this second leaf occupies an area placed diagonally to the longitudinal axis and surrounding the primordial meristem like a collar; scale = 0.1 mm.

FIG. 4. Ten-day-old seedling; as the first leaf is thrust out far from the cotyledonary sheath into the air the cotyledon elongates and curves downward until it is parallel with itself and the vertical shoot, having passed through an angle of 180 degrees; scale = 1 cm.

FIG. 5. Thirty-seven-day-old seedling; *b*₁ is the base of the first leaf, *l*₁, and *l*₂ is the second leaf; scale = 1 cm.

FIG. 6. Primordia of the thirty-seven-day-old seedling; scale = 0.1 mm.; *l*₄ and *b*₄ should be transposed.

FIG. 7. Diagram showing relative proportions of epidermal cells, raphide-bearing cells, starch-bearing cells and vascular traces; scale = 0.22 mm.

PLATE 15

FIG. 8. Longitudinal section (not quite through center) of thirty-seven-day-old bulb; note young root cutting way through base of the first leaf; this root arises at the third node and at the base of the second leaf; scale = 0.1 mm.

FIG. 9. Primordia of the fifty-four- to sixty-day-old seedling shown in FIG. 14; not a central section; scale = 0.1 mm.

FIG. 10. Longitudinal section (not central) through slightly developed plant to show region, *h*, dividing shoot and root in its early formation; *l*₁ is the first leaf.

FIG. 11. Primordia of bulb shown in FIG. 15.

FIG. 12. Detached young "offset" with two scales already formed; it arises from between the mature scales as a protrusion.

FIG. 13. Young "offset" which has pierced the outermost scale of the bulb; root contraction in old bulb not indicated; leaves and roots diagrammatic; scale = 5 cm.

PLATE 16

FIG. 14. Fifty-four- to sixty-one-day-old seedling. The cotyledon has become shriveled up and dead. As the first leaf is surrounded by the basal sheath of the cotyledon, so this second leaf sheath is surrounded by the basal sheath of the first leaf, in respect to which it is distichously placed; see Fig. 9; scale = 1 cm.

FIG. 15. Longitudinal section of thirty-one-day-old bulb; see FIG. 11; scale = 0.1 mm.

FIG. 16. Longitudinal section (not central) of thirty-one-day-old bulb; b_3 and l_3 are the points at which the primordia of the third leaf are forming; otherwise the symbols are as in preceding drawings; scale = 0.1 mm.

FIG. 17. Longitudinal section (not central) of thirty-seven-day-old bulb; l_4 is the fourth leaf, not a central section; the puckered or wrinkled condition of the primary root is due to contraction, a normal phenomenon; the outlay of root tissue has a narrow slice marked off into three sections—1, 2, and 3—for details of which see FIG. 19; scale = 0.1 mm.

FIG. 18. Longitudinal section through thirty-seven-day-old seedling with a young root showing a well-differentiated root cap and primary tissues (dermatogen, periblem and pleurome); scale = 0.1 mm.

FIG. 19. Showing under high-power magnification the root tissues laid off between the numbers 1-3 in FIG. 17; for further explanation consult text; scale = 0.1 mm.